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# The functional adaptations of mammalian brain structures through a behavioural ecology lens

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# [H1] Abstract

The organization of the extant mammalian brain is influenced by development, evolutionary history, and the environment. Ecological adaptations specifically have played a major role in shaping the structures and associated functions of the mammalian brain. Though general organization of the brain is relatively conserved in modern mammals, throughout millions of years of evolution mammals have acquired diverse sensory and nervous system adaptations as they invaded new ecological niches. Here, we synthesize paleontological and neurobiological evidence on mammalian brain structure evolution, the mechanisms behind the observed variation in the size and organization of brain structures and the impact of behavioural ecology on the evolution of brain functions and associated structures. Neuroecology has advanced greatly over the last 40 years and is now unravelling the complex relationship between specific behaviours and brain organization and function. Relying on different types of data, comparative neurobiologists and paleontologists strive to answer similar questions about brain evolution, benefiting from a synergistic approach. We conclude this Review by outlining outstanding questions regarding the relationships between structure, function, behaviour, and evolution that deserve future research attention, and propose methodologies and approaches to help resolve these problems.

# [H1] Introduction

Mammalian brain structures have been influenced by many different factors, including developmental and genetic constraints1, evolutionary history and phylogeny[2,3], the laws of physics[4], body morphology[5] and the environment in which an organism develops and lives[6]. The environment has been particularly crucial in the emergence of size and organizational variations in brain structures. Mammals occupy a wide range of habitats associated with a diverse suite of complex behaviours; they swim, fly, burrow, leap, run and climb, in habitats occupying land, water and the air[7]. As a result, mammals have acquired diverse neurosensory adaptations over millions of years of evolution by invading ecological niches that were either new or previously used by other vertebrates[8,9].

Integrating both paleontological and neurobiological data can further researchers' understanding of how brain structures evolved, the mechanisms behind the variation observed among brain structures and the impact of behavioural ecology on brain functions. Neurobiology provides valuable soft tissue information, not available in fossils, and facilitates the appreciation of how brain structural organization and interconnectivity are related to behavioural adaptations in a wide range of extant species[10]. However, problems might arise when inferring ancestral states from comparative studies of extant species. It can be difficult to disambiguate whether similar structures in different species are homologous or convergently evolved, particularly if only a few species are being compared. Osteological proxies for soft tissue (for example, the imprint of the endocranial cavity or brain endocasts) can be used to navigate this problem, such as those found in fossils, and can often be used to infer the ancestral condition[11]. By integrating data obtained from neurobiological and paleontological approaches, more accurate ancestral state reconstructions can be derived that account for the rich morphological information available in extant species, while correctly identifying instances of convergence or parallelism within the fossil record. By focussing on the influence of behavioural ecology, researchers can understand how particular features have emerged over the course of evolution in contrast to how these features emerged, which is the province of developmental studies. However, excepting birds, the relationship between behavioural ecology, brain structure and function has not been well studied in vertebrates[12].

In this Review, we describe the emergence and diversification of major mammalian brain structures and their associated functions, informed by extant and extinct species data. We then discuss potential mechanisms behind this neuroanatomical diversity by reviewing the allometric and evolutionary models that help explain the relationships observed between brain structures, overall brain size and body size. We specifically explore how ecological adaptations shape variations in the relative size of brain structures. We consider evidence that brain functions might be altered via behavioural changes, indirectly leading to changes in the size of brain structures. Finally, we emphasize the advantages of using a multidisciplinary approach to study the impact of behavioural ecology on the evolution of the mammalian brain. This Review focusses exclusively on terrestrial mammals, which experience very different evolutionary and ecological constraints compared to aquatic mammals.

# [H1] Evolution of mammalian brain diversity

A detailed understanding of the evolutionary history of the mammalian brain and its components is essential for exploring its potential evolutionary drivers. In this section, we integrate paleontological and neurobiological evidence to describe the evolution of the mammalian brain, the functional role of its structures, and discuss ongoing debates about the evolution of the neocortex and cerebellum

## [H2] Origin and organization of the mammalian brain

Around 90% of mammalian species that have existed on Earth are now extinct[13,14], but modern mammals are a combination of both ancestral and derived features. The fossil record and an understanding of relationships between extinct and modern species can be used to identify instances of evolutionary convergence and parallelism[3]. Considering both paleontological and neurological data, the gross brain organization of mammals appears to be relatively similar across both extinct and extant taxa, indicating that the first mammals probably had a similar Bauplan **[G]** [15], with some potential exceptions described later. Ancestral state reconstructions derived from modern species suggest that the organization of some structures was likely present in early mammals, such as topographic organization of sensory areas and ubiquitous patterns of thalamocortical connections[16]. Generally, the mammalian brain has olfactory bulbs, a cerebrum and cerebellum with varying degrees of folding, a midbrain, and a brainstem continuous with the spinal cord. The earliest mammals likely had the same organization but without folds (fissures) in their cerebrum and cerebellum[17,18]. The dorsal region of the cerebrum, the neocortex, is considered a mammalian innovation in comparison to other brain structures, and has been changed dramatically in both size and organization over the course of mammalian evolution. Specifically, the neocortex represents an expansion of the dorsal cortex that all amniotes possess[19].

The telencephalon of the amniote **[G]** ancestor that synapsids **[G]** share with sauropsids **[G]** was composed of a pallium (olfactory cortex, hippocampus, and dorsal pallium) and subpallium (basal ganglia)[20,21]. The fossil record indicates that the olfactory bulbs were the first region to expand in the synapsid lineage, followed by the cerebrum, before true mammals emerged[22]. In extant birds and mammals, the dorsal pallium has changed more dramatically in organization and size (specifically the neocortex and dorsal thalamus) compared to the olfactory cortex (including the olfactory bulbs) and hippocampus[19]. The dorsal pallium evolved into the neocortex in mammals (homologous to the Wulst in birds)[23,24], but remained mostly unchanged in other sauropsids[19]; however, the exact timing of this shift in the synapsid lineage is still uncertain because of the lack of evidence of a neocortex in early synapsids. As living sauropsids diverged from mammals more than 300 million years ago, fossil stem taxa **[G]** that are more closely related to the crown clade **[G]** of mammals than to sauropsids will be more informative in determining when this shift occurred (Fig. 1). However, a key challenge lies in identifying the boundary of the neocortex with the olfactory cortex using the rhinal fissure, which is not always preserved in fossils. The rhinal fissure was likely present in Cretaceous (143–66 Million of years ago[25]) mammals[26], but not in non-mammal synapsids, suggesting that the expansion of the neocortex might have occurred after mammals diverged from other synapsids[27]. Other regions of the brain are closely linked to the neocortex via shared signalling pathways. One of these regions is the dorsal thalamus, part of the diencephalon, that sends sensory inputs from the periphery to the neocortex, but this structure is also part of the transthalamic pathway in which specific nuclei receive descending cortical inputs and in turn project back to other cortical areas[28]. Thus, it likely follows that with the expansion of the neocortex in mammals, the thalamus also increased in size[2,29]. This hypothesis is solely based on studies of extant mammals because the thalamus does not leave a clear imprint on the endocranial surface.

Cortical expansion in mammals has been driven by changes in cell cycle kinetics, and in primates these changes have occurred to an exceptional degree[2,30,31]. For example, while mice and humans share many progenitor cell types, as well as specific aspects of cell cycle kinetics during neurogenesis, humans have an expanded outer subventricular zone and have evolved a new cell type called intermediate progenitor cells[32,33]. While developmental studies can uncover the mechanisms by which the neocortex or other brain structures have changed in size and organization, they cannot explain when in a clade's evolutionary history these changes emerged. Hence, demonstrating the value of integrating of the fossil record with neurobiological data on extant mammals.

Other structures of the brain appear to have changed less drastically, likely because they often contain regions involved in fundamental biological functions such as heart rate, respiration, orienting and balance. Nevertheless, these brain regions do show some variation in their relative size and structure. The midbrain of mammals includes the inferior colliculi (auditory lobes of some sauropsids[29] and torus semicircularis in other vertebrates[34]) and superior colliculi (optic tectum of other vertebrates[35]). Cretaceous mammals are the only Mesozoic (252–66 Mya) synapsids showing a differentiated midbrain into two lobes, likely the superior colliculi[26]. According to observations from the fossil record, the midbrain might have independently expanded in different mammalian clades and in these cases, would represent a derived condition[36]. In extant mammals, the relative size and general organization of the midbrain shows some variation, especially in species that have unique sensory specializations, such as tree squirrels which relies heavily on visual cues for their arboreal lifestyle[37].

Within the vertebrate hindbrain, the cerebellum is the region that has changed most substantially, becoming quite elaborate in birds and mammals[18,38]. The expansion of the cerebellum might have first occurred in non-mammalian cynodonts and mammaliforms[22], but the expansion of the vermis[39] into its two hemispheres is unique to mammals. However, the exact timing of differentiation of the vermis into the cerebellar hemispheres remains unclear. Though all modern mammals have cerebellar hemispheres that are visible on endocasts of similar extinct mammals, these hemispheres are not apparent in the endocasts of multituberculates, a mainly Mesozoic group likely more closely related to therians than to monotremes (see ref.[40] for a review of multituberculate fossil endocasts, but see also ref.[41]). Therefore, the expansion of the cerebellar hemispheres could have either evolved in parallel between therians and monotremes or have reduced in size in multituberculates[42]. Ultimately, CT scanning of more Mesozoic mammals will likely be key to resolving uncertainties about the timing of the emergence and expansion of the neocortex and the potential parallel evolution of the cerebellar hemispheres.

[H2] Mammalian brain structures and function

The neocortex is involved in processing and integrating incoming sensory inputs, perception, decision making and other higher order functions, such as language in humans[43]. Small brained mammals (such as rats and short-tailed opossums) tend to have around 15-20 cortical fields, while large brained species (such as humans) could have up to 300 cortical fields[2,16,44]. The functional organization of different cortical fields has been described in a rather restricted subset of mammals (including monotremes, and some species of marsupials, rodents, bats, and primates)[10,19]. Comparative data indicates that an array of cortical fields is common to all mammals studied and includes the primary visual area (V1), the second visual area (V2), the primary somatosensory area (S1), the second somatosensory area (S2) primary auditory area (A1) and motor cortex (M1)[45,46] (Fig. 2). Even when there is no evidence for the use of a specific cortical field, such as a primary visual cortex in blind mole rats, this cortical area can still be defined histologically[16]. It is likely that this array of cortical fields are homologous, inherited from the common ancestor of all mammals.

Despite the shared origins of these cortical fields, alterations of the functional organization, relative size and connectivity of these cortical fields have been identified in different mammals. These changes are associated with unique sensory specializations, along with morphological and behavioural adaptations[10,16]. For example, the duck billed platypus has evolved electrosensory reception mediated by specialized electroreceptors in its bill, and the primary somatosensory cortex is dominated by the representation of electroreceptors and mechanoreceptors of the bill[49]. Echolocating microchiropteran bats have an enlarged A1 as well as other auditory fields specialized for this unique behaviour. Primates with opposable thumbs evolved the fine motor control of the digits necessary to manipulate objects, and M1 is dominated by representations of muscle synergies required to engage in precision grips[50,51]. In Egyptian fruit bats, M1 has large representations of movements of the shoulder, hindlimb and ankle as an adaptation to flight. These bats also have an enormous representation of movements of the tongue in M1, which might be associated with the tongue clicks they use to echolocate, as well as their frugivorous lifestyle[52].

Although estimating the size of cortical fields in the fossil record cannot be done directly, the size and of sulci **[G]** might be used as indicators to broadly separate cortical regions. In arctoid carnivores, the postcruciate and cruciate sulci are expanded with secondary branches[53]. In raccoons, red pandas and coatis specifically, S1 has large representations for the forelimb and forepaw[54,55] in which each finger occupies a separate gyrus **[G]** , and this enlarged representation has been linked to fine control of the digits necessary for the manipulation of objects[56]. The endocast of the fossil mustelid *Promartes* has relatively well developed postcruciate and cruciate sulci[57,58], which suggests that this cortical field specialization associated with fine control of the digits could already have been present 16-23 million years ago (early Miocene). There are some limitations, because specimens with lissencephalic **[G]** brains including Mesozoic and many Cenozoic (66 Mya–present) mammals lack sulci. However, the surface of brain endocasts has been used to quantify the expansion of cortical regions without the use of sulci. This approach allows for the inclusion of lissencephalic brains, but only broad functions can be inferred[59,60]. One important caveat is that the relationship between brain surface and cortical field expansions remains underexplored. The inferred expansion of the visual cortex in Oligocene (23–34 Mya) squirrels and Eocene (34–56 Mya) primates is based on the assumption that it is directly linked to the expansion of the caudal region of the neocortex covering the midbrain[61,62]. However, this pattern could be caused by the expansion of other brain regions pushing the visual cortex in the caudal direction.

The other brain structures that can be studied from both paleontological and neurobiological perspectives have diverse functionalities. The size of the olfactory bulbs is correlated with an enhanced sense of olfaction and strongly associated with ecology[63-65]. The fossil record indicates that the ancestor of mammals had relatively large olfactory bulbs and olfactory cortex relative to other brain regions and likely relied more on olfaction than on other senses[3,15,26]. The status of the olfactory system in extant monotremes is varied. The platypus, which has specializations associated with electroreception (as mentioned previously), has relatively small olfactory bulbs and pyriform cortex and does not appear to rely heavily on olfactory-mediated behaviours in its semiaquatic environment. By contrast, echidnas have a specialized olfactory system including large, gyrencephalic olfactory bulbs and a relatively large pyriform cortex[66]. Echidnas rely on olfaction for finding mates, food sources and navigating in their large home ranges (0.02 km$^2$ to 3.56 km$^2$)[67]. More generally, ancestral state reconstructions recover substantial shifts in olfaction in various mammalian clades, including a decrease in olfaction in early primates[3,68].

The midbrain is another structure that can be imprinted on endocasts. The superior colliculi are involved in visual orienting and eye movements, whereas the inferior colliculi participate in sound localization, startle response and auditory orienting[69]. Colliculi are not always visible on the endocranial or brain surface as they might be covered by the neocortex, the cerebellum or sinuses[59,62,70]. Notably, laryngeal echolocating bats have enlarged inferior colliculi (and auditory cortex, as mentioned previously), which can be visible on the surface of the brain[71-73]. The fossil record indicates that the colliculi were larger than the neocortex in early mammals[26] suggesting that they used to play a major role in visual and/or auditory processing. The endocranial anatomy of the Oligocene fossil caviomorph *Incamys* suggests that it might have had enlarged inferior colliculi, linked to enhanced auditory capabilities and social behaviour[74]. Finally, the petrosal lobules (paraflocculi of the cerebellum[75]) located inside the subarcuate fossa relate to the control and smooth pursuit of eye movements[76]. In fast moving extant mammals, the petrosal lobes are larger, implying that their function might be enhanced in comparison with animals moving more cautiously[6,59,75,77] (but see [78]). Some Cretaceous mammals, such as the multituberculates *Kryptobaatar* and *Litovoi*, had relatively large petrosal lobules[41,79], indicating a potentially higher reliance on these structures compared to earlier members of this lineage.

[H1] Shaping the evolution of the brain

The size of the brain and body must be considered when quantifying brain structures and their evolutionary pathways in extant and extinct species. In this section, we review the potential mechanisms shaping the relative size of brain structures. Finally, we show that the mosaic and concerted models act at different taxonomic levels and therefore are not mutually exclusive.

[H2] The allometry of the brain and of major brain regions

To conjointly use paleontological and neurological data to determine the evolutionary drivers that have shaped the mammalian brain, the size of brain regions must be quantified. Brain regions are linked to specific functions that are often distributed across networks composed of multiple brain regions[10,80,81]. How this type of organization arose over the course of evolution remains unclear, but as noted prior, the relationship between structure and function is intrinsically linked to morphological and behavioural specializations. This association can be explored by examining the allometric relationships between brain, body and brain structure sizes in different mammalian species[82]. Allometry is a useful tool for paleontologists because it is a reliable way to test whether a structure might be relatively larger in some species versus others by relating the size of structures relative to body size[83,84]. This approach is also widely used in neurobiology to study the relationships between the mass of different brain regions, the size of cortical fields or the number of neurons in specific structures[2,52,85]. Brain regions such as the neocortex, olfactory cortex, and cerebellum are correlated with brain size in many mammalian clades and exhibit distinct allometric relationships[1]. However, it is not always clear why allometric relationships exist, and why some groups (or species) deviate from these relationships[82,86,87]. Equally important considerations are why some brain regions have an allometric relationship and appear to be co-evolving with other regions of the brain[2,88], and what are the underlying principles by which this co-evolution occurs.

Generally, brain size increases with body size in extant mammals[1]; however, over the course of evolution, this scaling relationship has changed with modern species exhibiting larger brains compared to extinct species of similar body size (indicating a temporal effect on brain size)[3,89]. From the Paleocene (56–66 Mya) to the end of the Eocene, brain size increased more than body size. More specifically, this relative increase in brain size was the result of the expansion of the neocortex and the petrosal lobules[3]. These structural size changes in relation to brain size could reflect a functional shift[90]. However, this pattern might also be the result of a proportional change and not a true change in the size of a given structure, and thus not a change of its function[84,91]. For example, from the Paleocene to the Eocene, the size of the olfactory bulb decreased in relation to brain size, but not in comparison to body size. This suggests that other regions of the brain have increased in proportion (for example, the neocortex), but the actual size of the olfactory bulb has remained stable (Fig. 3a). In contrast, clades such as Eocene Primates show a reduction in size of the olfactory bulbs relative to brain and body size, suggesting a real decrease in the size of these structures. Because the size of brain structures have been associated with function (see previous section), this suggests a reduction in olfaction in Eocene Primates [3] (Fig. 3b). In cases where brain structures are not correlated with body size, the actual size (without controlling for overall brain or body size) can be used to deduce function[74].

These examples underscore the importance of comparing brain structures to both brain and body size, and of exploring trends in both a clade-specific and taxonomically inclusive manner. Allometry is not sufficient to describe the relationship between function, structure and behaviour alone. Nevertheless, it provides a useful framework to study how brain structures responsible for diverse behaviours vary in their relative functional importance.

## [H2] Mosaic versus concerted models of evolution

Two key hypotheses have been proposed to explain the allometric relationships and variation observed in mammalian brains[85,92,93]. The concerted evolution model proposes that the brain is a single integrated unit, and that all brain regions are linked together by developmental processes (for example, rate and duration differences in the development of brain regions). This model connects similar brain variations to important ontogenetic events (such as duration of neurogenesis and axonal branching patterns[94,95]). Under this model, allometric relationships are due to the order of neurogenesis for different brain structures that appear highly conserved in mammals[87]. For regions that are relatively larger than others (for example, the neocortex), the model proposes that this is due to a faster rate of growth of these components. For example, while the thalamus increases with brain size, the neocortex increases at a faster rate[2]. Though there is clear evidence for concerted evolution, this model cannot explain selection for adaptive behaviour that alters specific regions of the brain.

By contrast, the mosaic evolution model proposes that the brain is an aggregation of subunits that are not linked to one another. Under this model, a brain structure might change because an associated behaviour was selected for, while the rest of the brain remains unchanged[82,86,96]. Support for the mosaic model as a driver of ecological specialization can be found in in fish[97,98], reptiles[93,99], birds[92] and mammals[6,86,96]. In relaxed versions of the mosaic model (that is, more than one region can vary), brain regions might be either developmentally linked, as in the concerted model, or functionally connected[92]. For example, functional links have been found between structures that have a similar function and therefore co-vary such as olfaction (olfactory cortex and olfactory bulbs) and vision (lateral geniculate nucleus and visual cortex)[96]. The presence of developmental constraints helps maintain the corresponding functionality of two structures. However, it can be challenging to disentangle what type of constraints link brain components, as both can act simultaneously on the brain and result in similar changes. This complexity makes it difficult to evaluate why diversity in brain regions emerged in modern mammals. One approach is to focus on the contribution of either development or function to the evolution of the brain of organisms. For example, the division of the brain of primates into functional categories instead of structures (such as visual, olfactory, gustatory and spatial cognition), leads to a more complete understanding of the socioecological factors responsible for the observed size covariation among brain regions[86]. Finally, connections between two brain structures covarying in size might disappear because the behaviour produced by the associated connected brain regions has been lost[82]. For instance, the olfactory and visual brain structures are positively correlated in bats, while the opposite is true for primates. The observed decrease in olfaction and increase in vision in primates suggests a behavioural or functional shift that resulted into these brain structures changing independently from one other[100]. This interpretation is further supported by the fossil record evidence of a decrease in olfactory bulb size and an increase in optic canal size in primates[68,101].

While the same data might be used to evaluate both the concerted and the mosaic models of evolution, the major difference between the two models relates to the taxonomic rank of study. Considering trends across Mammalia, examples of concerted evolution represent deep brain homologies and likely play a substantial role in shaping covariation in brain regions. For example, intercladal trends in Placentalia exemplify the allometric relationship between the neocortex and the thalamus[2] (Fig. 3d). Each clade appears bound by specific developmental constraints. However, within specific clades such as eulipotyphlans, slight deviations from their cladistic regression line can be observed. These smaller deviations correspond to mosaic evolution. For example, species belonging to Sciuridae show strong deviations from their total clade regression for the relative size of the olfactory bulbs and the petrosal lobules, which have been linked to different locomotor behaviours[6,62] (Fig. 3c). Therefore, the concerted evolution model demonstrates that the brains of eulipotyphlans or rodents are constrained by distinct developmental profiles, leading to limited options for diversity. However, the mosaic model illustrates that deviations in the size of brain structures linked to specific ecological niches might arise within each of these clades.

[H1] Integrative approaches to brain evolution

Modern approaches are changing the ways that neuroecologists study the relationship between brain structures, functions and behavioural ecology. In this section, we explore these approaches and emphasize the need to systematically consider the evolutionary history of extant mammals when investigating the link between brain evolution and ecology.

## [H2] Behavioural ecology and brain functions

Throughout decades of studying the external factors impacting the brain of mammals, a recurrent issue has been defining the ecology of mammals and its impact on the size and organization of brain structures. In the last ten years, the link between the size of brain structures and functions with ecology has been increasingly studied, but sampling remains limited and targeted to specific clades such as primates, rodents, bats and lagomorphs (Supplementary Table 1). Some general patterns between brain structure sizes (such as olfactory bulbs and petrosal lobules) and ecological categories (including diet, locomotion, diel pattern) have been identified. For instance, large olfactory bulbs might be related to a frugivorous diet and nocturnality, whereas large petrosal lobules can be related to locomotor behaviour (Supplementary Table 1)[6,64,75,100,102]. These trends might reflect some deep causal relationships between the brain and its environment; however, interpreting these correlations is not straightforward and, in many instances, it might not be sensible to treat them as causations.

As noted previously, there is not a one-to-one relationship between brain structures and specific functions: multiple regions of the brain form networks that generate function, and any given region in that network might also be part of another network involved in a different function[103]. Therefore, instead of testing the ecological impact on a brain structure, testing the impact on a brain function might provide more convincing evidence for a link between brain changes and the environment. However, this prospect still evades the ecological aspect that must be considered, demanding a clearer definition of how function and ecology are linked, such as how vision relates to arboreality. These two categories, vision and arboreality, were created as they are easy to analyze and can generally be applied to a wide array of species. However, these categories were not designed to test the adaptability of specific brain functions. Many arboreal mammals have distinct morphological, sensory and behavioural adaptations[104]. These animals’ reliance on vision could be reflective of multiple factors, with some of them not being uniquely linked to living in trees, such as finding food, finding mates, or escaping from a predator. In contrast, navigating among tree branches is a trait specific to arboreal fauna.

An integrative neuroecological approach which accurately defines specific brain functions and associated behavioural ecologies will continue to benefit researchers seeking to understand how behaviour might drive brain evolution[12,105]. However, gathering comparable behavioural data for a wide range of species is complicated. Most behavioural datasets represent captive animals in a highly controlled environment such as the ongoing collection of behavioural audiograms[106,107]. However, animals did not evolve in laboratory environments and comparisons of wild caught and laboratory animals find significant quantifiable disparities in features of brain, such as the density of neurons found in visual cortex[108]. Similarly, rats reared in seminatural conditions demonstrate differences in both motor cortex organization as well as behaviour involved in the coordination of the limbs when compared to rats bred in a laboratory setting[109]. One of the best examples of the relationship between ecology, morphological and behavioural specialization, and cortical organization and function is the star-nosed mole (*Condylura cristata*), the fastest known forager among mammals. This mole has evolved specialized nose appendages (the star) which contain Eimer's organs. This tactile fovea allows the animal to detect small changes in the shape and texture of a stimulus, such as small objects or prey in their subterranean habitat[110]. The representation of the star is magnified in the somatosensory cortex and contributes to the remarkable behaviours exhibited by this mammal[111].

Sensory ecology describes the way an animal interacts with the surrounding environment, and is a useful tool in exploring the relationship between behaviour, ecology, and the brain[112] (Box 1). Modern neuroecological research has primarily focused on birds including, for example, the variation in the size of the hippocampus and its function (spatial memory) with food hoarding (behaviour)[12]. Additionally, given the large constraints imposed by species evolutionary history, a particular behavioural phenotype might not be the only target of selection. Rather, plasticity itself (the ability to generate adaptive behaviour in a dynamic and changing environment) could be the driver behind brain evolution. There is some evidence that changes in behaviour might precede changes in morphology[113], but questions remain regarding the correspondence between the size of brain structures and how they are linked to an organism's behavioural ecology. For example, diurnal and/or frugivorous primates have a larger primary visual area (V1) than other primates[86]. However, this enlargement might not be due to foraging colored fruits, because nocturnal primates also rely on vision to find food using moonlight[114]. Despite the idea that enhanced colour vision would be an advantage for finding fruits, behavioural observations have shown no difference in foraging efficacity between dichromat **[G]** and trichromat **[G]** individuals[115,116]. The size variation of V1 in primates might be related to factors other than foraging, such as depth perception, or even social interactions[114]. To improve our understanding of the drivers behind brain structure size changes, more work needs to incorporate both behaviour and neuroecology.

## [H2] Integrating neurobiology, paleontology and behaviour

Species' evolutionary history is critically important when attempting to understand the impact of ecology on the brain evolution of mammals. Using osteological proxies, the behavioural ecology of extinct species can be reconstructed. For instance, before the discovery of early fossil aplodontiids, the fossorial adaptations of the mountain beaver were thought to represent the ancestral condition for Sciuroidea. However, the fossil record indicates that the ancestor of squirrels and mountain beavers was likely an agile tree dweller, suggesting that the fossorial adaptations of the mountain beaver are a derived state[117,118]. Consequently, when interpreting brain structure size and organization, it must be noted that this brain first evolved for an arboreal environment. Arboreal adaptation is a very deeply rooted trait in squirrel evolution that was already present 35 million years ago[119] (Fig. 4a). Modern tree squirrels have an expanded visual cortex with multiple cortical fields (Fig. 4b, 4c), and likely have good depth and color perception, with strong visuomotor integration necessary to move in the three-dimensional space of the trees. This adaptation heavily contrasts with other non-arboreal rodents, particularly the naked mole rat, which spends all its life underground where vision is not crucial for survival, and has very little of the neocortex (if any) devoted to visual processing[10]. The size of brain endocast regions in extant and extinct species supports the hypothesis that arboreality had a fundamental impact on the brain evolution of squirrels. Ancestral state reconstructions indicate that an increase in the size of the petrosal lobules and neocortex coincided with the acquisition of an arboreal lifestyle in squirrels[6] (Fig. 4a). Inferring functional roles from the brain of extant squirrels, this increase in size is indicative of enhanced eye movement control, and potentially better color vision, depth perception, spatial location and optic flow in early squirrels. The opposite appears to have occurred in the lineage leading to extant mountain beavers as they rely less on vision because of their fossorial specialization[6], informed by the smaller visual cortices observed in extant fossorial mammals[10]. Crucially, modifications of brain regions are built upon structural organizations of ancestors that likely evolved under different selective pressures driven by ecological adaptation[120].

The evolution of bats (Chiroptera) is another example that underscores the value of using a combined approach to understand the impact of echolocation and diet on their nervous system. There are two types of echolocation in extant bats: laryngeal echolocation and tongue clicking echolocation. Laryngeal echolocation varies considerably, including deviation in frequency, and these bats can also be nasal or oral emitters[121]. Postcranial remains of the earliest bats demonstrate that they were already capable of flight 52 million years ago[122,123]. Concerning echolocation, the inner ear of the stem bat *Vielasia* was adapted to laryngeal echolocation and this bat was likely an oral emitter, suggesting that the ancestor of crown bats had similar adaptations[124,125]. This indicates that nasal emittance in laryngeal echolocators, tongue click echolocation and non-echolocation are derived conditions in extant bats, and thus that their respective neurosensory adaptations were built from an oral-laryngeal echolocating bat ancestor. Nevertheless, it is crucial to keep in mind that even bats with this ancestral type of echolocation are likely to be extremely specialized, as the origin of bats occurred over 50 million years ago[126] and members of this lineage have been independently evolving for a very long time. Few brain endocasts have been published for bats. A nasal emitting fossil hipposiderid bat (*Palaeophyllophora*) shows highly expanded inferior colliculi[90] similar to extant bats with the same echolocation type[73]. Taken together, Paleogene (23–66 Mya) bats likely relied heavily on audition and were echolocating.

In addition to echolocation, diet appears to have had a huge impact on sensory evolution in bats. Ghost bats, for example, are insectivorous nasal emitters with an expanded auditory cortex that has been associated with echolocation[127,128]. Compared to insectivorous bats, frugivorous bats have larger olfactory bulbs[64,100], likely because their plant-based diet requires olfactory foraging[129]. Frugivorous bats have independently evolved olfactory receptor genes that others bats lack[130] and the flying fox (a non-echolocating bat), for example, has a larger visual cortex, likely associated with foraging colored fruit[131]. The fossil record, however, suggests that frugivory is likely derived in bats, and ancestral bats might have been insectivores[132]. The olfactory bulbs of *Palaeophyllophora* do not appear especially large, indicative of a non-frugivorous diet. In the same species, a relatively short caudal part of the neocortex suggests a small visual cortex, offering further evidence that these bats did not rely heavily on vision for foraging[90].

## [H1] Summary and future directions

The overall brain organization of mammals has been remarkably conserved; however, the structures within the brain exhibit notable variations in terms of their size and organization. Different factors have influenced the evolution of these structures including developmental constraints, common ancestry, and ecology. The concerted and mosaic models of evolution can both explain the observed variation, and they are not mutually exclusive. They function at different taxonomic levels, with the mosaic model applying better to lower taxonomic ranks than the concerted model. The field of neuroecology has evolved over the last 40 years by first focusing on the impact of broad ecological categories on the size of brain structures and neuron counts of specific brain regions. Today, the focus is on understanding the role of specific behaviours on brain functions, and ultimately on the size variation of associated brain structures. Throughout this Review, we highlight the importance of using both neurobiological and paleontological perspectives as complementary disciplines to study the evolution of brain structures in relation to behavioural ecology. However, there are many aspects pertaining to the influence of ecology on the brain that are not well understood and should be addressed in the coming years. Here, we suggest some of the most pressing issues for future consideration.

The relationship between brain structures and functions is not always clear, as one structure might be responsible for many functions[133]. For example, in humans, functional networks do not always overlap with structural networks[134]. Instead of using a one-to-one structure-to-function model, a strong correspondence has been identified between functional and structural modules[135]. This way of partitioning the brain should continue to be considered in future studies to improve understanding of the functional and structural connectivity of the brain, especially in non-human species. The utility of diverse imaging techniques such as functional magnetic resonance imaging (fMRI), electroencephalography (EEG), magnetoencephalography (MEG) and positron emission tomography (PET) as well as network theory and computational modeling cannot be overlooked. These techniques have been and will continue to be crucial to understanding the brain structure function relationship[133,136], especially in the study of active behaviour while recording brain activity[137]. Further, these non-invasive techniques allow for the study of key extant species that otherwise would not be available for invasive studies owing to ethical or conservation guidelines.

The association between behaviour and function require further interrogation, as the observed correlations between these variables might not always represent causation. Lesion, neural inactivation and stimulation studies will likely be required to improve causal inferences[138]. However, alternative neurofeedback approaches (such as variant of task-based neuroimaging) are also promising. This non-invasive method measures how brain functions correlate to specific behaviours. Under this approach, brain activity is modified, which leads to behavioural change, and allows a stronger test of causality[139,140]. For example, in birds, task-based neuroimaging approaches have enabled researchers to identify direct links between food hoarding, spatial memory and its associated brain structure, the hippocampus[141]. Future behavioural studies also have to consider the Umwelt **[G]** of the animal[112] when generating questions and experiments, as species likely experience the world very differently from humans. Researchers must also consider the impact of anthropogenic change on the behaviour of extant animals, especially those that show major differences when compared to behavioural classifications recorded in the literature (such as activity diel in mammals)[142].

Regarding paleontological integration, the ancestral states of brain structures for diverse mammalian clades are not well understood. Furthermore, brain structures and functions might have evolved in ancestors with very different ecological and behavioral demands than those imposed on extant species. It also remains unclear if various behaviours in distantly related species with superficially similar ecologies are homologous[143]. One important step to overcoming these issues is to continue to collect brain and behavioural data on a wider range of species to avoid falling into the trap of assuming shared ancestry. Online repositories such as Morphosource[144] already include a vast database of scanned specimens (such as the oVert project[145]) to generate virtual brain endocasts. Non-invasive fMRI[146] and comparative work of extant species that involve other *in vivo* methods (such as electrophysiology, architecture, and neural connections) will continue to improve researchers' understanding of neocortical diversity. Continuing to expand this understanding in species beyond laboratory animals is essential to facilitate exploration of the link between behaviour and brain structure in a biodiverse array of species, such as sociality in freely moving bats[147].

From a behavioural standpoint, compiling behaviours related to specific ecologies will be crucial. Convergence in arboreal-related behaviours is widespread in vertebrates[148], but the correspondence between these behavioural adaptations and brain structures has not been explored at a large scale. Regarding the fossil record, skeletal elements and trace fossils will continue to be important behavioural proxies[149].

Ultimately, a multidisciplinary approach that considers different levels of organization from brain structure and function to behavioural ecology and macroevolution will improve reseachers' comprehension of the brain diversity present in mammals today. At this stage, the field is still earnestly gathering data, but in the coming years, these data might enable modelling studies elucidating the causes behind these co-variations in brain structures.

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## Competing interests

The authors declare no competing interests.

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## Supplementary information

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## Figures

**Figure 1: The evolution of mammalian brain structure.** Animals are illustrated alongside their brain endocasts where available. Endocasts are not to scale, and delimitations of the regions are approximations. The brain endocast for *Dimetrodon*[159] is incomplete and was not illustrated. The midbrain was only illustrated when it was identifiable on the surface of the endocast. Stem group Mammalia are illustrated with a blue star. Crown clade Mammalia are denoted with a red star. *Tachyglossus*, *Didelphis* and *Sciurus* are extant taxa representatives of their respective mammalian clades and are not illustrated concordant with their divergence time. Phylogenetic tree topology and clade age based on refs.[22,160,161]. Brain endocasts estimations based on data from refs. [15,21,26,40,79,162-164].

**Figure 2: Organization of the mammalian brain**. **a**, Organization of the brain at the embryonic developmental stage in humans. **b**, Organization of the brain at the adult stage in mouse (top) and human (bottom), not to scale. Homologous structures are coloured accordingly. Large size differences are apparent in the olfactory bulbs and the neocortex. **c**, Neocortical map organization in different mammalian clades. Neocortices not to scale. Part b is adapted from ref.[166], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Part c adapted with permission from ref. [10], Karger Publishers.

**Figure 3: Brain structure size trends. a,** Residuals from a Phylogenetic Generalized Least Squares (PGLS) regression of Olfactory bulb volume versus Endocranial volume (top), and Olfactory bulb volume versus Body mass (bottom) for mammals from the Mesozoic, Paleocene, Eocene stem taxa, and Eocene crown orders. **b,** Ancestral state reconstruction of residuals in part a mapped onto a phylogenetic tree of Euarchontoglires. **c,** Phylogenetically corrected PGLS regressions of petrosal lobule volume versus body mass for different locomotor behaviours in Sciuroidea. **d,** Regression of Neocortex volume versus thalamus volume in a biodiverse sample of mammals. Where not indicated, volumetric measurements are in cubic millimeters, body mass is in milligrams. All size data are log10 transformed to normalize for body size. Parts a and b adapted with permission from ref. [3], American Association for the Advancement of Science. Part c is adapted from ref. [6], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Part d adapted with permission from ref. [2], Elsevier.

**Figure 4: Cortial architecture trends in squirrels. a**, Ancestral state reconstruction of neocortical surface area as a percentage of the brain in Sciuroidea and extinct relatives, including virtualised brain endocasts for two representative fossil squirrels, *Cedromus* and *Protosciurus*. **b**, Schematic representations of cortical architecture for two species of extant squirrels, *Sciurus carolinensis* and *Otospermophilus beecheyi*. **c**, Percentage of the dorsolateral cortex devoted to somatosensory/motor, auditory, and visual areas in *Sciurus carolinensis* and *Otospermophilus beecheyi*. Error bars represent the standard error of the mean. The asterisk denotes a significant difference ($p<0.05$). Abbreviations: A1, primary auditory area; A17, area 17; A18, area 18; AAF, anterior auditory field; M1, primary motor cortex; OT, occipital temporal area; PV, parietal ventral area; R, rostral field; S1, primary somatosensory area; S2, second somatosensory area; TA, temporal anterior area; TP, temporal posterior area. Part a is adapted from ref [6], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Parts b and c adapted with permission from ref. [10], Karger Publishers.

## Box 1: Sensory organs and osteological proxies

Sensory ecology is the study of how environmental information is detected and processed, and how the organism responds to this information[167]. Sensory organs include the eyes, ears, nose, tongue and skin, and transduce physical stimuli into neural signals and then relay this information to the brain. The sensory organs of a species are adapted to specific ecological niches and play a role in survival and reproduction[168-170]. For instance, very distantly related clades such as toothed whales and microchiropteran bats can both use high-frequency echolocation sounds, while elephants and baleen whales use very low-frequency sounds to communicate[171-174]. Species can have visual specializations adapted to see more effectively during the day or night[175,176]. Regarding olfaction, some species are considered macrosmic relying intensely on the sense of smell (rodents and carnivores) or microsmic in which this sense could be reduced (some primates) or lost (cetaceans)[177]. Sensory organs can sometimes work co-operatively, with potential trade-offs present. For example, mammals that live in trees generally have larger eyes and smaller noses in comparison to terrestrial species, implying that the evolution of the senses are highly correlated[178].

The fossil record does not routinely preserve soft tissues such as the sensory organs; however, some osteological proxies can be used to estimate their sizes or shapes and provide significant insight into the senses and behaviours of extinct taxa. One of the most widely studied sensory organs is the inner ear, with key roles in audition, balance and angular head velocity[179-181]. Endocasts of the inner ear provide information on how these senses evolved in fossil mammals[182-184]. For olfaction, the cribriform plate and the nasal turbinate (also rarely preserved) can be used. The cribriform plate likely evolved in basal mammals, suggesting enhanced olfactory sensitivity in early members of this group[15,22]. The orbit size and the size of the optic nerve has been used for estimating vision in fossil primates[101,185]. The infraorbital foramen size for the branch of the trigeminal cranial nerve (CN V) has been used to estimate tactile sensitivity of the snout in fossil euarchontans[186]. The acquisition of whiskers, used for collecting spatial information in the environment, could be linked to the evolution of the maxillary canal into the infraorbital foramen in mammalian ancestors[187]. The proxies of these various sensory organs can be coupled with the study of the brain to improve researchers' understanding of the behaviour organisms in deep time.

## Glossary

**Crown clade:** Monophyletic group of species that share a common set of morphological features. It includes all the living representatives of a given group, their common ancestor and all its descendants.

**Stem taxa:** Paraphyletic group of species that lack some characteristics found in the crown clade. For example, stem mammals are considered the closest relatives to the clade Mammalia.

**Bauplan:** General structure of the body or region of the body plan that characterizes a group of organisms such as the brain of Mammalia.

**Amniote:** Group of tetrapod vertebrates that has evolved an amnion, a closed sac filled with amniotic fluid that surrounds the embryo, allowing its development outside of water.

**Synapsids:** Group of amniotes that includes the crown clade Mammalia and their closest extinct relatives including the pelycosaur *Dimetrodon*.

**Sauropsids:** Group of amniotes that includes the crown clades birds, crocodiles, turtles and lepidosaurians (tuataras, lizards, snakes, and amphisbaenians) and their closest extinct relatives including non-avian dinosaurs.

**Sulci:** Grooves on the surface of the brain. Complex sulci pattern emerges as brain size increases.

**Gyrus:** Ridge between sulci of the brain. When taken together, they form a system of complex folding pattern. Brains with folding are known as gyrencephalic brains.

**Lissencephalic:** Characterizes brains that do not present any sulci on their surface.

**Dichromat:** Defines organisms that can only distinguish two primary colors. The condition present in most mammals.

**Trichromat:** Defines organisms that can distinguish all three primary colors. This is most widespread condition in humans.

**Umwelt:** Represents the unique way in which organisms perceive the world. This perception will be shaped by the kind of information that can be processed by their sensory organs.

## TOC blurb

Palaeontologists and comparative neurobiologists share a common interest in the evolution of the mammalian brain, but often fail to realize the benefits of this shared interest. This Review draws these fields together, demonstrating the utility of a cross-disciplinary, synergistic approach.